First records of the order Siphonophorida from Madagascar and Mauritius (Diplopoda)

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First records of the order Siphonophorida from Madagascar and Mauritius (Diplopoda). - The first records of the colobognathan millipede order Siphonophorida from Madagascar and Mauritius are presented. Specimens representing both families of the order, Siphonophoridae and Siphonorhinidae, were discovered on Madagascar. The specimens were collected from 18 rainforest and montane rainforest localities using primarily the Winkler or Berlese extraction methods. The limited number of specimens (mostly less than 5) available from each site and the difficult taxonomic state of the order prevented the naming of any of the specimens. Specimens from one locality could be studied in more detail using SEM. and were tentatively determined as members of the Asian genus Siphonorhinus Pocock, 1894, presently known only from Asia. Four additional Siphonophorida samples representing at least two different species came from three localities on Mauritius, providing the first record of the order from the island. All Siphonophorida specimens should be carefully examined before taxonomic description attempts, as some might represent widespread tropical tramps.

Keywords: human introduction - rainforest - Siphonorhinus - Siphonorhinus.

INTRODUCTION

With its 115 described species in an unknown number of genera (Jeekel, 2001), Siphonophorida is one of the least species-rich of the 16 orders of millipedes, class Diplopoda (Blanke & Wesener, 2014). The order includes not only the two leggiest millipede species (*Illacme plenipes* Cook & Loomis, 1928 with 750 legs, *Siphonophora panamensis* Loomis, 1961 with 742), but also those with the highest intraspecific segmental variation observed so far, a variation between 25 and 182 segments (Shelley & Hoffman, 2004; Read & Enghoff, 2009). The present concept divides Siphonophorida into two families, the more basal Siphonorhinidae, whose representatives still have discernible mouthparts (Attems, 1938; Fig. 1C), and the Siphonophoridae, whose representatives have a head that has been strongly modified into a sucking organ with a beak (= rostrum) and a very small opening. The majority of species in the order (104 of 115) belong to the Siphonophoridae.

The distribution of the order was recently reviewed (Shelley & Golovatch, 2011). Representatives of the order Siphonophorida inhabit the northern half of South America, Central America up to California and Texas, eastern South Africa, the Seychelles, Sri Lanka, the Himalayas, Southeast Asia, eastern Australia, New Zealand and several pacific islands. They are notably absent from Europe, northern Asia and Africa except for eastern South Africa. Here we report the first representatives from Madagascar and Mauritius.

Siphonophorida has been regarded as a taxonomist's nightmare (Hoffman, 1980) and received the hypothetical award for the least popular order of millipedes (Jeekel, 2001). It gained this reputation mainly because of the apparent lack of characters allowing generic- and species-level distinctions, and because of the huge number of insufficiently described species (including 48 nomina dubia in *Siphonophora* alone; Jeekel, 2001). The latter are often based only on one or a few specimens, mostly females. Descriptions of Siphonophorida species are difficult because, as representatives of the subclass Colobognatha (Blanke & Wesener, 2014), adult males continue to moult and grow, which leads to conspecific males of different sizes, showing a gradual development of the taxonomically important gonopods (Shelley & Hoffman, 2004).

There is little knowledge about the general morphology of the order, and that which exists is scattered (but see Hoffman, 1982; Read & Enghoff, 2009). Even basic questions regarding the absence or presence of defensive secretions and their potential chemical compositions remain unanswered.

The family Siphonorhinidae (with only 11 known species) will be relatively simple to revise, as recent integrative studies have been conducted (Marek *et al.*, 2012). Siphonophoridae, despite an important revision (Shelley, 1996), remains nightmarish. A first study of taxonomic characters of the Siphonophoridae was conducted recently (Read & Enghoff, 2009), but even though it included large series of two species and used scanning electron microscopy, no good taxonomic characters were discovered. The gonopods seem to be uniform, and setation seems to vary intraspecifically. The only characters that allow a distinction between species were the lengths of the beaks (= rostra), the colour, and length/width ratio, the latter of which is dependent on the size of the specimen.

With this in mind, and especially considering the possibility that some species of Siphonophoridae might be widespread tropical pests, the reader can understand why I currently refrain from naming any Malagasy forms, all of which are known only from at most a handful of specimens.

MATERIAL AND METHODS

ILLUSTRATIONS: Multi-layer photographs were taken of the specimens from Manjakatompo (MHNG Mad-89/21) with a Leica Z6 Imaging-System based at the ZFMK. Stacked images were put together using the software Auto-Montage (Syncroscopy). The specimen examined using scanning electron microscopy was carefully dissected under an Olympus SZX12 stereo-microscope with Dumont #5 Inox forceps. The samples were then dehydrated via an ethanol chain, mounted on stubs and dried overnight. The stub was sputter-coated with 100 nm of gold in a Hummer VI (Anatech, USA) sputtering system. Images were obtained using a Hitachi S-2460 SEM.

All images were later modified using Adobe Photoshop version CS2 and assembled onto plates using Adobe Illustrator version CS2.

MUSEUM ACRONYMS: CAS - California Academy of Sciences, San Francisco, California, U.S.A. FMNH - Field Museum, Chicago, Illinois, U.S.A. MHNG - Muséum d'histoire naturelle de la Ville de Genève, Geneva, Switzerland. MNHN - Muséum National d'Histoire Naturelle, Paris, France. ZFMK - Zoological Research Museum A. Koenig, Bonn, Germany.

RESULTS

SPECIMENS FROM MADAGASCAR DETERMINED TO GENUS-LEVEL

Siphonorhinus sp.

Fig. 1

MATERIAL EXAMINED: MHNG Mad 89/21; 3 &, 2 \(\rho_1 \); Madagascar, Province Antananarivo, Ankaratra massif, Station Forestière Manjakatompo, près du sommet du Anosirivo, forêt primaire, prélèvement de sol dans une vieille souche, 1980 m; 26.xi.1989, leg. B. Hauser, extraction Berlese à Genève.

HABITAT: The forest of Manjakatompo is one of the three last (99% has been destroyed) indigenous high plateau forests on Madagascar. It was planted by humans a few centuries ago, when it was still connected to now no longer existing fragments of pristine highland vegetation. It harbours rare and endemic genera and species of mammals, but lacks other faunal elements (such as lemurs) most likely due to the artificial origin of the forest and the lack of any fruit-bearing trees (Goodman *et al.*, 1996).

REMARKS: Largest specimen (male) about 11 mm long, 0.7 mm wide, with 61+1 segments. Colouration whitish orange (Fig. 1A). Only specimens of this species could be studied in more detail. While the author refrains from a formal description. the illustrated characters can be compared with those of properly revised species (Shelley & Hoffman, 2004; Marek et al., 2012) to allow a revision of the family in the future. This species is only tentatively placed in the genus Siphonorhinus Pocock, 1894, whose eight species occur in Indonesia, Vietnam, Cambodia, Laos and India (Jeekel, 2001). Siphonorhinus is characterized by an unmodified first leg in males where the coxa is fused to the sternite or stigmatic plate (Fig. 1B), by a pear-shaped head (Fig. 1C), and by the apical podomere of the posterior gonopod being divided into two branches lacking spines (Fig. 1D). In the South African genus Nematozonium Verhoeff, 1939 the posterior gonopods are different, with one of the branches wrapped around the second branch and with each of the branches carrying a spine (Shelley & Hoffman, 2004). The species of the other Asian genus, Kleruchus Attems, 1938 (originally assigned to the order Platydesmida), are much larger and wider, and feature thick modified first legs in males. The fourth genus, Illacme Cook & Loomis 1928, is known only from California, USA. It resembles the shorter species presented here, and features different, apically serrated posterior gonopods (compare Fig. 1D to Marek et al., 2012: fig. 6a).

SPECIMENS FROM MADAGASCAR DETERMINED ONLY TO FAMILY LEVEL

Siphonorhinidae Cook, 1895

The family Siphonorhinidae is characterized by a pyriform, subtriangular head that is not extended into a rostrum, devoid of macrosetae (Fig. 1C). Head with discer-

nable mouthparts, especially mandibles (Attems, 1938). Antennae bent between antennomeres 3 and 4, pits of sensory cones on articles 5 and 6 absent, only a field of sensilla basiconica present (Fig. 1C). Containing 11 species grouped in four genera (Siphonorhinus, Illacme, Nematozonium and Kleruchus), distributed in California, South Africa and southeastern Asia (Jeekel, 2001).

MATERIAL EXAMINED: FMNH-INS 4000; 1 $\,^{\circ}$, 1 immature; Madagascar, Province Fianarantsoa, R. S. Ivohibe, 8 km east of Ivohibe, camp II, 22.4833°S, 46.9683°E, 1200 m, montane rainforest; coll. B. L. Fisher, 15.-21.x.1997, Winkler extraction. Remarks: Colouration light brownish white. Body densely pilose with long setae. – FMNH-INS 8012; 1 $\,^{\circ}$; Madagascar, Province Toliara, Réserve Naturelle Intégrale d'Andohahela, parcelle 1, 20.0 km SE Andranondambo, 24.5617°S, 46.7217°E, 1875 m, montane rainforest; coll. S. M. Goodman, 27.xi.-05.xii.1995. Remarks: Colouration whitish, densely pilose, with short setae. – FMNH-INS 8036; 1 immature; same data as for FMNH-INS 8012. Remarks: Probably same species as FMNH-INS 8012. – FMNH-INS 8012. Remarks: 1 $\,^{\circ}$ with eggs. Probably same species as FMNH-INS 8012. – FMNH-INS 8125; 1 $\,^{\circ}$; Madagascar, Province Fianarantsoa, 40 km S Ambalavao, Rés. Andringitra, 22.2167°S, 46.9667°E, montane rainforest; coll. B. L. Fisher, 15.x.1993, Winkler extraction. Remarks: Colouration brown, with patches of white. Densely pilose with short setae.

Siphonophoridae Newport, 1844

Siphonophorida characterized by a head extended into a sharply acuminate 'beak' or rostrum, lower half of it formed by gnathochilarium. Head with four macrosetae. Antennae straight, not elbowed, antennomeres 5 and 6 with large, conspicuous pit containing numerous sensory cones (Hoffman, 1982). Antennomere 2 of normal length. 104 species in ten genera distributed in America, SE Asia and the Indian subcontinent (including N Pakistan), Australia and New Zealand (Jeekel, 2001).

MATERIAL EXAMINED: FMNH-INS 3978; 1 ♀; Madagascar, Province Antsiranana, R.S. Manongarivo, 20.4 km SW Antanambao, 14.0467°S, 48.4017°E, 1860 m, montane rainforest; coll. B. L. Fisher, 03.xi.1998, Winkler extraction. Remarks: Colouration marbled greyish, body short and densely pilose. — FMNH-INS 4089; 1 ♂; Madagascar, Province Antsiranana, Befingotra (9.2 km WSW), Rés. Anjanaharibe-Sud, 14.7500°S, 49.4667°E, 1280 m, montane rainforest; coll. B. L. Fisher, 05.xi.1994, Winkler extraction. Remarks: Colour similar to FMNH-INS 3978.

SPECIMENS FROM MADAGASCAR ONLY DETERMINED TO ORDER LEVEL

The following specimens were regretfully only sorted to order level. A re-examination of the listed specimens was not possible during the course of this study.

MATERIAL EXAMINED: MNHN "81"; 2 specimens; Madagascar, 1957, 296, Fanovana; 13.vii.1957, P.A. Remy. – MNHN "101"; 1 specimen; Madagascar, 1957, 295, Fanovana. Remarks: Potentially Province Toamasina, Fanovana, 18.9250°S, 48.533°E, 720 m, rainforest, now degraded. –MNHN "83"; 1 specimen; Madagascar, 1957, 238, Manjakatompo; 4. juillet 1957, P.A. Remy. – MNHN "85"; 1 specimen; Madagascar, 1957, Manjakatompo, forêt ancienne vers 1800-1850 m; juillet 1957, P.A. Remy. Remarks: Potentially Province Antananarivo, Manjakatompo/Ankaratra, 19.3667°S, 47.3000°E, 1800 m, montane rainforest. – MNHN "94"; 1 specimen; Madagascar, 1957, 285, Perinet; 5.viii.1957, P.A. Remy. – MNHN "95"; 1 specimen; Madagascar, 1957, 285, Perinet; 5.viii.1957, P.A. Remy. – MNHN "86"; 1 specimen; Madagascar, 1957, 287, Perinet; 17.viii.1957, P.A. Remy. – MNHN "93"; 1 specimen; Madagascar, 1957, 252, Tsinjoarivo; 11.vii.1957, P.A. Remy. – MNHN "87"; 1 specimen; Madagascar, 1957, 251, Tsinjoarivo; 17.vii.1957, P.A. Remy. Remarks: Potentially Province Toamasina, Tsinjoarivo/Fenerive-Est, 17.0500°S, 49.1333°E, 500 m, rainforest. – MNHN "96"; 3 specimens; Madagascar, 1957, 316, Ambodihatafana; 27.viii.1957, P.A. Remy. Remarks:

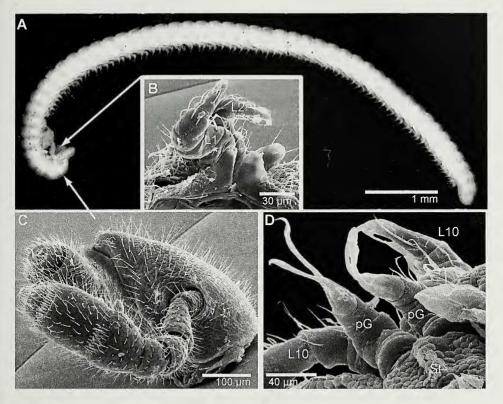


FIG. 1

Siphonorhinus sp., MHNG Mad 89/21, two males, A = smaller male specimen, B-D = largest male specimen, multi-layer photograph and SEM. (A) Habitus, lateral view. (B) First and second legs, anterior view. (C) Head, lateral view. (D) Posterior gonopods and leg pair 10, anterior view. Abbreviations: L1 = leg 1; L2 = leg 2; L10 = leg 10; pG = posterior gonopod (= leg 9); St = sternite fused to stigmatic plate.

Potentially Province Toamasina, Ambodihatafana, 16.21666°S, 49.4333°E, 795 m, rainforest, now degraded. - MNHN "99"; more than 5 specimens; Madagascar, 1957, Ambila Lemaitso; fin viii.1957, P.A. Remy. Remarks: Potentially Province Toamasina, Ambila-Lemaitso / Andevoranto, 18.8167°S, 49.1333°E, 16 m, coastal rainforest, now degraded. – CAS BLF 7385; 1 specimen; Madagascar, Province Fianarantsoa, Forêt d'Analalava, 29.6 km W Ranohira, 22°35'30"S, 045°07'42"E, 700 m, tropical dry forest; coll. Fisher, Griswold et al., 1.-5.ii.2003, vellow pan trap, Remarks: 1 & black. - CAS BLF 10501; 7 specimens; Madagascar, Province Toamasina, Ambatovy, 18°51'03"S, 48°19'17"E, 1075 m, montane rainforest; coll. Malagasy ant team, 21.iii.2004, sifted litter (leaf mold, rotten wood). - CAS BLF 10502; 9 specimens; Madagascar, Province Toamasina, Analamy, 18°48'22"S, 048°20'13"E, 1068 m, montane rainforest; coll. Malagasy ant team, 21.iii.2004, sifted litter (leaf mold, rotten wood). Remarks: Elongated, whitish, small. – CAS BLF 10627 MW; numerous specimens; Madagascar, Toamasina, Torotorofotsy, 18°52'15"S, 48°20'51"E, 1070 m, montane rainforest, marsh edge; coll. Malagasy ant team 24.iii.2004, sifted litter (leaf mold, rotten wood). - FMNH-INS 3990; 1 specimen; Madagascar, Province Fianarantsoa, 8.0 km NE Ivohibe, camp IV, 22.4217°S, 46.8983°E, 1200 m, montane rainforest; coll. B. L. Fisher, 03.-09.xi.1997, pitfall traps. -FMNH-INS 3997; 1 specimen; Madagascar, Province Toliara, S.F. Mandena, 8.4 km NNE Tolagnaro, 24.9522°S, 47.0017°E, 20 m, littoral rainforest; coll. B. L. Fisher, 20.xi.1998, Winkler extraction. - FMNH-INS 13727; 3 specimens; Madagascar, Province Fianarantsoa, 38

km S Ambalavao, Rés. Andringitra, 22.2000°S, 46.9667°E, 1680 m, montane rainforest; coll. B. L. Fisher, 22.x.1993, Winkler extraction. – FMNH-INS 104157; 1 specimen; Madagascar, N of Ambalarondro, 18.41556°S, 48.97136°E, 405 m, rainforest; coll. K. Emberton, 25.ix.2009. – FMNH-INS 104519; 3 specimens; Madagascar, Sahafina, 10 km W of Brickaville, 18.8167°S, 48.9764°E, 186 m; coll. K. Emberton, 19.iii.2009.

SPECIMENS FROM MAURITIUS ONLY DETERMINED TO ORDER LEVEL

MATERIAL EXAMINED: MNHN "98"; more than 5 specimens; 1957, 352 u. 353, Le Vallon [Volton?]; 24.09.1957, P.A. Remy. – MNHN "84"; 1 specimen; 1957, Cocotte; 29.ix.1957, P.A. Remy. – MNHN "88"; 1 specimen; 1957, 390, Triamon; 9.x.1957, P.A. Remy. – MNHN "92"; 3 specimen (two different species, one with short, one with elongated rostrum!); 1957, Ile Maurice; sept.-oct. 1957, P.A. Remy. – MNHN "97", several specimens, Ile Maurice; sept.-oct. 1957, P.A. Remy.

DISCUSSION

Siphonophorida are apparently widespread in the lowland rainforests and montane rainforests of Madagascar, having been collected from 18 sites spanning most of the humid biome on the island (Fig. 2). The existence of both families, Siphonorhinidae and Siphonophoridae, is a further indication of the natural occurrence of the order on Madagascar. Surprisingly, most of the studied specimens of both families seem to be relatively small and much shorter than the large and multisegmented record holders recently redescribed from South Africa (Shelley & Hoffman, 2004) and North America (Marek *et al.*, 2012). Siphonophorida, however, seem to be relatively rare and elusive on Madagascar, with only few individuals, always five or less, discovered per site, often by means of Winkler and Berlese extractions.

Although millipede inventories have been conducted on Mauritius (Verhoeff, 1939, 1941; Mauriès & Geoffroy, 1999), previously referred to as "Ile de France", I here record for the first time the occurrence of the order Siphonophorida on the island. The Mauritius specimens come from at least three sites, belong to at least two different species and were found stored among the Madagascar material collected by P. A. Remy (Remy, 1956) at the MNHN. Because a relatively high number of introduced millipede species inhabit Mauritius (Mauriès & Geoffroy, 1999), the possibility exists that one or two siphonophoridan tramp species may also have been spread by humans. An analogous situation is found in the siphonotid polyzoniidan *Rhinotus purpureus* (Pocock, 1894), which now occurs on most (all?) continents (Shelley, 1998; Wesener, 2014). The possibility of widely introduced siphonophoridans constitutes a good reason why new species in the order should be described only with careful illustrations of the male gonopods and other potentially taxonomically important characters in order to avoid synonyms.

Currently, there is only one established system for the Siphonophorida, the family-level division into Siphonophoridae and Siphonorhinidae which dates back to the 19th century. Anything below that systematic level is in its infancy. A proper taxonomic foundation is lacking. In the near future I hope to provide a more detailed morphological description of the family Siphonorhinidae based on the Malagasy Siphonorhinus species pictured here. Hopefully, once large series of specimens become available for study, the taxonomic characters of species and genera can be resolved on the basis of molecular data. This process has begun for the only American represen-

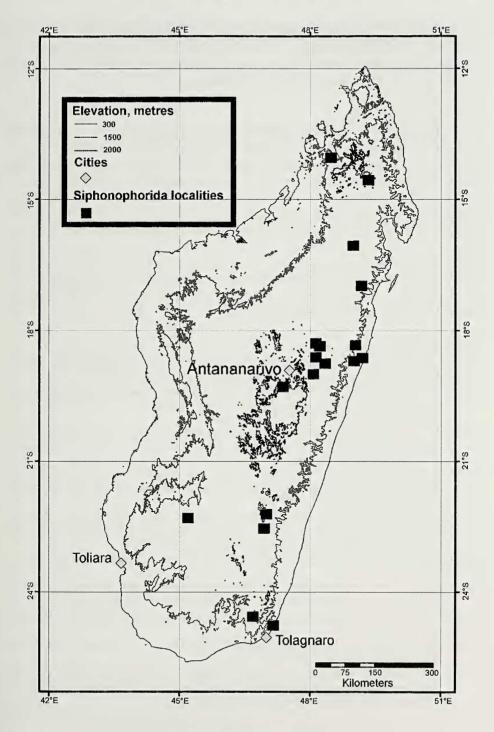


Fig. 2 Distribution of Siphonophorida localities on Madagascar.

tative (Marek *et al.*, 2012). After taxonomic characters have been established, especially in the Siphonophoridae, the backlog (Jeekel, 2001) of old types can be reexamined and assessed. This would enable the description and naming of new species without the risk of creating additional synonymies.

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